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LARVAL DEVELOPMENT OF THE GIANT SCALLOP *PLACOPECTEN MAGELLANICUS* (GMELIN) [1]

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The giant sea-scallop, *Placopecten magellanicus* (Gmelin) ranges along the east coast of North America from Labrador to Cape Hatteras (Abbott, 1954). Although primarily a continental shelf species, it may be found one meter below low tide in the Gulf of Maine (Read, 1967). At the southern end of its range, off North Carolina, *P. magellanicus* generally occurs in water over 150 feet (46 meters) deep (Porter, 1974).

A regional fishery for *P. magellanicus*, chiefly off New England and eastern Canada, has stimulated some research on the biology of this scallop including studies of length-weight relationships and gonad development (Haynes, 1966); thermal tolerances and acclimation (Dickie, 1958); and growth rates in different geographical regions (Stevenson and Dickie, 1954 and Merrill, Posgay and Nichy, 1966). Up to the present, however, research on the giant scallop has been confined to the adult stage. The dearth of information concerning larval biology of *P. magellanicus* has formed a conspicuous gap in knowledge of the life history of this species.

The purpose of this paper is to describe the complete larval development of *P. magellanicus*, including observations on larval salinity tolerance and settling behavior. Information derived from rearing larvae in the laboratory may help to confirm the identification of *P. magellanicus* larvae from the plankton and will aid future mariculture efforts with this valuable food species.

Materials and Methods

Sexually mature scallops were collected by SCUBA diving at Isles of Shoals, New Hampshire on September 21, 1973. They were placed in sea water in a styrofoam chest and held for 8 hours at approximately 5° C until returned to the laboratory. I selected small adults (3″–5″ diameter) to minimize stresses to the animals from confinement in limited volumes of water both during transport and in subsequent spawning containers in the laboratory.

Males and females were separated for spawning, which was stimulated thermally by raising the temperature 3–5° C. Gametes and developing larvae were generally handled as recommended by Loosanoff and Davis (1963) and Culliney, Boyle and Turner, (1974).

Larvae were reared in cylindrical glass jars containing two liters of sea water filtered to remove particles larger than one micron in size. The sea water was changed every two days. Salinity during development was nearly constant at

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32‰, and was measured with hydrometers. Dilutions for the experiment on salinity tolerance were made using filtered pond water.

The naked flagellate, *Isochrysis galbana* Parke was used to feed larvae up to the settling stage. Spat have been reared using a combination of *I. galbana* and *Chroomonas salina* Taylor. Concentrations of algal food ranged from approximately 50,000 cells/ml in cultures containing the youngest veligers to 5,000 cells/ml as larvae approached the pediveliger stage. Young spat, however, were fed concentrations approximating 10,000 cells/ml.

Measurements of larvae were made using a calibrated ocular micrometer. Clean shells of pediveliger larvae were prepared by feeding live larvae to small sea anemones. After the empty shells were egested by the anemones, right and left valves were teased apart so that the hinge structure could be observed and measurements made of individual valves.

Antibiotics were not used until larvae reached the pediveliger stage. Then 50 ppm Sulmet (sodium sulfamethazine) was added to all cultures to arrest an apparent necrotic disease.

Results

Spawning

One diver in our party observed spawning in the undisturbed population from which adults used in this study were taken; he reported seeing a scallop suddenly emit a puff of milky material. On the day of collection, September 21, 1973, the temperature of the bottom water (about 50 feet deep) was 14° C; that of the surface was 16° C. Many captured scallops of various sizes (2″–8″ diameter) spawned profusely in buckets of sea water within minutes after they were brought to the surface.

In the laboratory, some individuals spawned readily within minutes after the temperature was raised from 5° C to 10° C. Others were held in large bowls of aerated filtered sea water at 12° C. A number of these spawned two days later when the water temperature was raised to 15° C.

In all, two minor and two major spawnings were cultured from separate groups of individuals. The minor spawnings were not reared past the early veliger stage due to low numbers and deformities of the larvae. Each culture was produced by a different female and several males. Cultures from different spawnings were not mixed; several populations of a convenient two-liter size were set up from each of the two major spawnings.

Development of larvae

The main features of development are summarized in Table I. Development to the earliest swimming stage occurred at 12° C in all populations and lasted between 30 and 40 hours. The embryos first became motile as ciliated gastrulae averaging 69 microns long and 63 microns across the greatest diameter. They appeared to elongate slightly into a trochophore-like stage, then became typical shelled straight-hinge veligers (Fig. 1) on the fourth day after spawning. Young straight-hinge larvae possessed a very short apical flagellum. The mean size of the earliest straight-hinge larva was 105 microns long by 82 microns high. The

hinge line averaged 81 microns. (In the following description, shell dimensions will be given as length × height in consistent order.)

Development from the ciliated gastrula to the straight-hinge stage occurred over the temperature range 12° C to 18° C. Such a thermal gradient, arranged vertically by setting culture jars in a shallow cold-water bath, allows the motile larvae to seek their optimum temperature during the thermally sensitive period of straight-hinge shell deposition (Culliney *et al.*, 1974).

Initially several populations of veligers were reared at two temperatures, 15° C and 19° C, but populations at 19° C did not complete development. Development was rapid with little apparent difference in growth rates at the two temperatures.

TABLE I.

Major features of larval development of Placopecten magellanicus *at 15° C, 32‰*

Stage or distinctive feature	Age	Mean size (μM)	Range (μM)	S.E. (μM)	N*	Remarks
Unfertilized egg	0	64	63–65		17	Color pink to brown Temp. 12° C.
Earliest swimming stage (gastrula)	30–40 hours	length: 69 diam.: 63	68–70 62–64	0.35 0.24	6 13	Temp. 12–18 °C.
Earliest veliger (straight-hinge)	4 days	length: 105 height: 82 hinge-line: 81	99–107 77–84 75–82	0.24 0.24 0.24	27 27 27	Temp. 15° C.
Loss of apical flagellum Umbo veliger	8 days 13–28 days	length: . . . . . . height:	175–264 155–232		61 61	Temp. 15° C.
Appearance of eyespot Bottom seeking behavior Development of foot Adhesive tendency	23 days	length: >230 height: >210				
Pediveliger (sporadic crawling, weak byssus, growth of gill rudiment)	28 days	length: 279 height: 242 depth: 127	266–292 238–254 110–142	0.94 1.64 1.40	46 46 20	Temp. 15° C.
Spat (extensive crawling, strong byssus, growth of dissoconch shell and gill)	>35 days					

* N refers to the number of individuals measured.

The tiny apical flagellum disappeared; it could not be detected by the eighth day. The hinge line remained visible and of nearly constant length until about the 13th day when larvae began to exceed 175 × 150 microns in size (Fig. 1).

Beginning on the 15th day, extensive mortalities were observed in populations at 19° C. By the 19th day, cultures at this temperature were nearly completely decimated. A fungus appeared associated with the mortality at 19° C, but was not seen attacking living larvae. Throughout this period, populations of larvae at 15° C appeared normal and showed almost no mortality.

During larval development, shell length remained 25–30 microns greater than height. A regression of length *versus* height, calculated from over 100 measurements of veligers in all stages of development, illustrates the quantitative relationship between the two dimensions: height = 0.96 length − 18.2.

The extended velum in swimming larvae had a unique "keyhole" outline. This was most pronounced in half-grown veligers. The outline of the velum tended to become nearly oval as larvae approached the pediveliger stage (Fig. 2a).

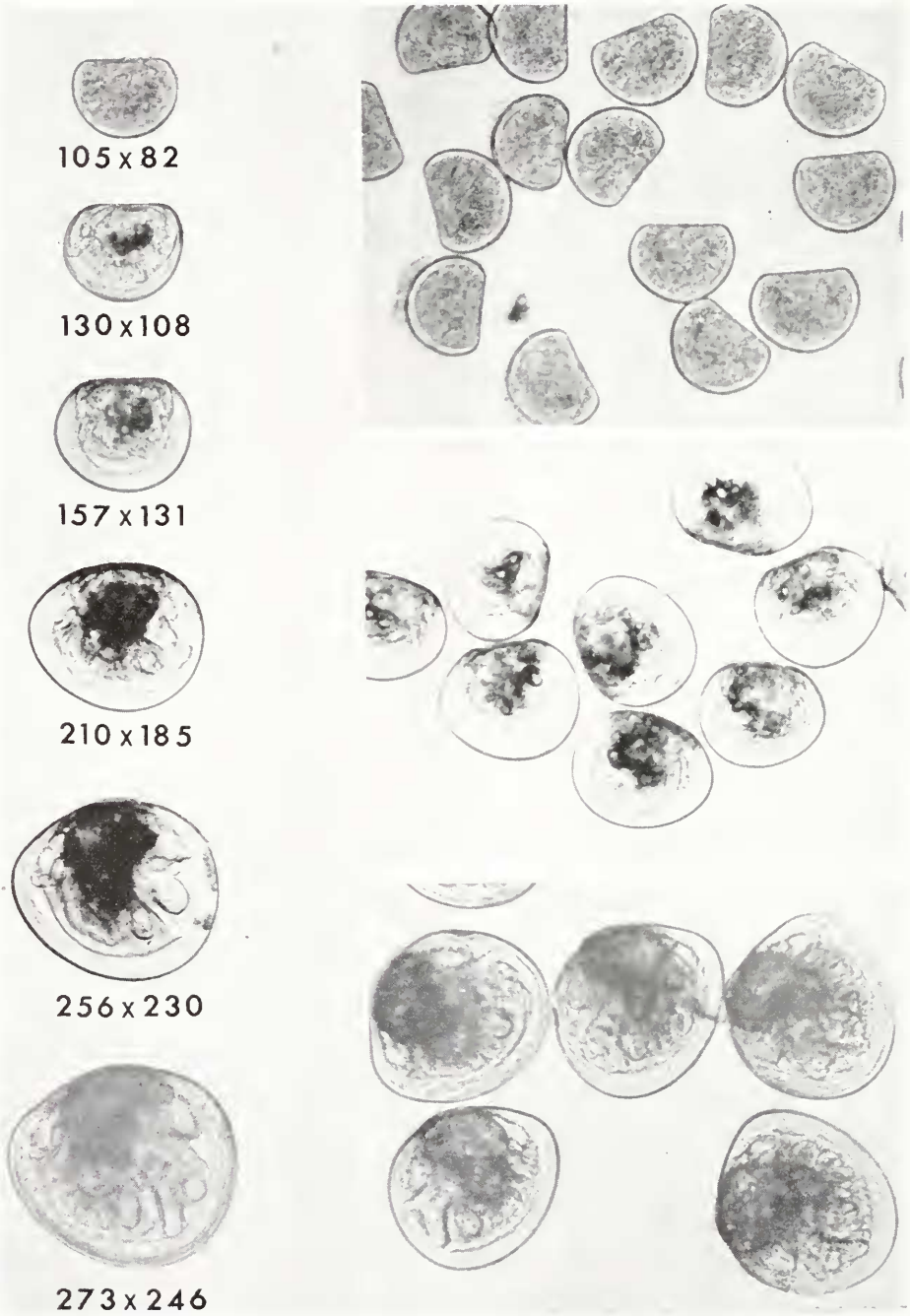


FIGURE 1. Individual and group photographs of *Placopecten magellanicus* larvae from the straight-hinge stage to the pediveliger (sizes in microns). The more pointed end, to the left in photos of individual larvae, is the anterior end.

The shape of the larval shell, standing on edge (Fig. 2b) revealed a slightly longer taper in the anterior than in the posterior direction. These features may have some taxonomic value.

On the 23rd day, typical bivalve veliger eyespots, such as occur in ostreid and mytilid larvae, were first noticed in larvae larger than 230 × 200 microns (Fig. 2c). By this time the larval foot had become prominent, although it was not yet observed extending outside the shell. In addition many larvae showed a change in swimming behavior. Prior to the 23rd day they were well dispersed in the water column, althought most swam in the upper third of the container. After the 23rd day increasing numbers of larvae were observed massed in dense swarms, swimming just above the bottom of the culture jar.

As larvae approached the pediveliger stage, they often displayed the foot as they swam. The most conspicuous feature of the foot was a cluster of long active cilia at its tip (Fig. 2d); also a well-formed heel or byssal spur was present. About this time, the larvae began to show an adhesive tendency, causing them to

TABLE II.

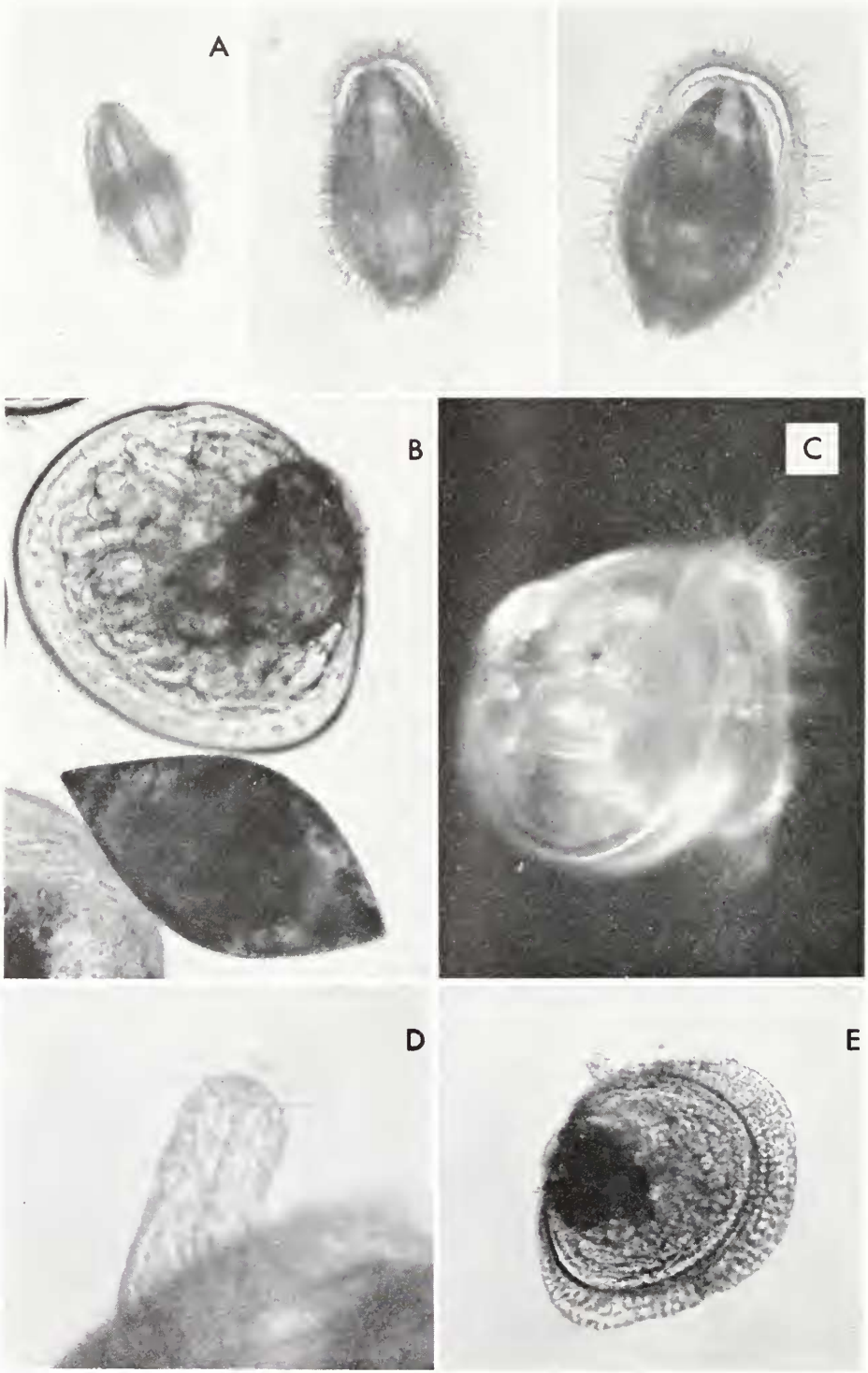
Dimensions of left and right valves of Placopecten magellanicus *pediveligers*

	Left valve				Right valve			
	Mean (μM)	Range (μM)	S.E. (μM)	N*	Mean (μM)	Range (μM)	S.E. (μM)	N*
Length	280	264–292	1.64	21	276	257–290	1.76	20
Height	254	232–268	1.88	21	250	230–264	1.76	20
Depth	67	50–76	1.38	21	60	48–70	1.40	20

* N refers to the number of individual values measured.

stick to each other and to dust particles, pseudofeces, and other debris. By the 28th day after spawning more than 50% of the larvae in all populations possessed the functional foot characteristic of the pediveliger stage. Pediveligers crawled readily, but for only short distances on glass slides and on the glass bottoms of culture containers. Crawling seemed to be initiated after larvae were disturbed. For example, brief episodes of crawling occurred when larvae were discharged from a pipette, or after they were sieved and placed in new culture containers. Pediveligers secreted a weak byssus which could not be seen readily, even when magnified at 100 ×. A prominent gill rudiment was present in most pediveligers (Fig. 2c). Average measurements of pediveliger larvae were 279 × 242 microns with a depth of 127 microns.

The hinge structure of *P. magellanicus* larvae was almost featureless. A series of minute taxodont teeth were present, but their actual number was not determined and good photographs of the hinge were not obtained. Pediveliger shells were difficult to separate, indicating the presence of a strong binding force, possibly a ligament, in the hinge area. Many shells cracked or fractured in the attempt to disarticulate them. A number of shells were separated into intact valve pairs, however, and measurements of these show that the left valve averages slightly larger than the right in length, height, and depth (Table II). The difference in depth between the two valves is statistically significant at the 95% level.


A
B
C
D
E

Effects of low salinity

A mixed population of umbo-stage larvae, originating from the two female parents, was tested for salinity tolerance over a 42 hour period. Twenty larvae were pipetted into each of five finger bowls containing 180 ml of water at salinities of 10.5, 16.9, 21.5, 26.2, and 30.0‰. (Salinity was measured after the experiment). The temperature was held at 15° C. No food was given during the experiment. The LD_{50} level for salinity could not be estimated for the conditions stated, since all the larvae survived the 42 hour experiment. However, the behavior of the larvae was recorded.

At 10.5‰, larvae remained on the bottom of the finger bowl. After an initial shock produced immobility for about two hours, most larvae remained moving during the experiment. However, normal swimming was not observed. Most larvae lay on one valve and rotated in place; they appeared incapable of retracting the velum which had a distended appearance. The color of the larvae remained normal. At 22 hours, six of the twenty larvae showed no movement when the distended velum was touched by a fine needle. But at 42 hours all larvae were moving vigorously.

At 16.9‰, an initial shock produced immobility for about two hours. However, many individuals recovered and exhibited normal swimming and translational movement, but they remained close to, often touching, the bottom.

At 21.5‰, an initial shock was evident, but most larvae regained full mobility within two hours. Most larvae remained swimming close to the bottom. One individual was seen well above the bottom, however, 15 minutes after the beginning of the experiment, and two individuals swam near the surface at 42 hours.

At 26.2 and 30.0‰, no alteration of larval behavior was noted. Larvae swam throughout the water column, but most remained near the surface, throughout the experiment.

Settling behavior

The first spat was found 35 days after spawning. A conspicuous feature of the spat was the presence of a strong, thick, plainly visible byssus (Fig. 2e), contrasting with the "invisible" threads produced by pediveligers. Crawling by spat was vigorous and extensive, and was observed predominantly after the byssus was broken. At least some settling individuals cast off the velum in large pieces. On several occasions a nearly complete detached velum was seen.

P. magellanicus, however, appeared to settle in culture containers only reluctantly. As pediveliger larvae accumulated and very few spat were found, it appeared that a delay of metamorphosis was occurring. Presumably this was due to the lack of an attractive substrate for settlement. Two experiments were set up to examine potential stimuli to settlement. These included presence of adult *P. magellanicus* shell material and general thigmotatic effects of three-dimensional surfaces. The results of these experiments are shown in Figure 3.

FIGURE 2. Special features of larval development of *Placopecten magellanicus;* (A) outline of the velum of swimming larvae from early umbo stage to the pediveliger (× 120); (B) comparison of horizontal and vertical shell profiles in late umbo stage larvae (× 180); (C) gill rudiment and eyespot in pediveliger (× 140); (D) tip of pediveliger's foot, showing tuft of long cilia (× 580); (E) spat with well-formed byssus (× 110).

The experiments utilized pediveliger larvae in 4-inch finger bowls containing 200 ml of filtered sea water. Twenty larvae were exposed to each settling stimulus. Controls were simply held in finger bowls without an added stimulus. The temperature was 13°–15° C. Larvae were fed 5,000 cells/ml *Isochrysis*. Experimental and control populations were examined every 3–4 days, and fully metamorphosed and dead individuals were removed. Criteria for metamorphosis were attachment by a strong byssus and complete absence of the velum. Individuals showing only one of these features were considered partially metamorphosed (not shown in Figure 3).

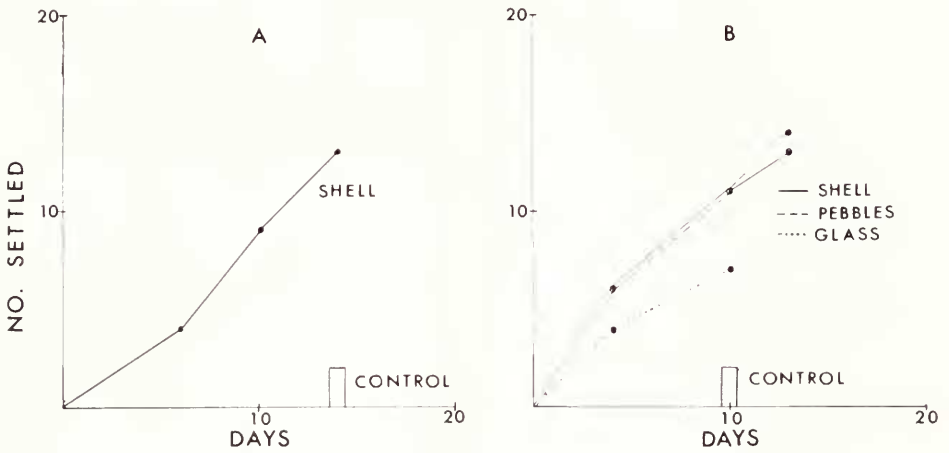


FIGURE 3. Cumulative plots of numbers of *Placopecten magellanicus* settling in response to different stimuli. Experiment B followed the completion of A. The single vertical bar in each plot represents metamorphosed individuals in the control populations.

Experiment A examined the reactions of larvae exposed to six fragments of fresh adult *P. magellanicus* shell. The fragments ranged from 3 mm to 2 cm long and were scattered on the bottom of the finger bowl. The results (Figure 3) show a strong settling response to the fragments. Thirteen larvae metamorphosed; two were partially metamorphosed at the end of the experiment, and three were dead. Settled larvae nearly always attached directly to the shell fragments and predominantly tended to metamorphose on the undersides of the fragments. Of the thirteen fully metamorphosed individuals, all but two were attached underneath the shell pieces, and only one did not attach to the shell. In the control, two larvae metamorphosed and one died.

An additional set of larvae was exposed at this time to increased food concentration (25,000 cells/ml *Isochrysis*. None of these larvae metamorphosed, indicating that increased food concentration is not an important settling stimulus. This result is omitted from Figure 3.

Experiment B attempted to separate properties of *Placopecten* shell as stimuli from a more general thigmotactic effect. The response to scallop shell fragments was compared to that induced by small pebbles and glass fragments. All of these objects were visibly clean but not sterile. Numbers of larvae and background

conditions were the same as in Experiment A. Experiment B followed the end of Experiment A.

The results (Fig. 3) demonstrate that a strong stimulus to settling and metamorphosis is provided by all classes of physical objects tested. In the case of shell fragments and pebbles, the results were nearly identical to those in Experiment A. There is, however, a slight indication that Experiment B larvae, two weeks older than those in Experiment A, were prone to settle more quickly on the stimulus objects. Mortality in the presence of shell fragments and pebbles was low and comparable to that in Experiment A.

The population of larvae exposed to glass fragments, pieces of a microscope slide approximately the size of the shell fragments, suffered an unusually high mortality (nine dead). However, metamorphosed individuals accumulated on the glass fragmens at a rate that paralleled the results with shell and pebbles.

Again in Experiment B, most metamorphosed individuals were found on the undersides of the objects tested. In the control population only two larvae settled.

Discussion

The successful rearing of *Placopecten magellanicus* may reflect the fact that adults were obtained in prime condition for spawning. One previous attempt during the winter, to condition adults to develop gonads and spawn failed. This large active scallop may need more food than normally can be supplied under laboratory conditions. Comely (1972), working with the large European scallop, *Pecten maximus,* also experienced failure in conditioning experiments. Previous attempts by other investigators to culture *P. magellanicus* larvae have also been unsuccessful. (P. Chanley, Shelter Island Oyster Co.; H. Hidu, Univ. of Maine, personal communication).

A number of purported difficulties at the time of spawning have been encountered by investigators rearing other species of scallops. These problems have included poor vitality of embryos resulting from self-fertilization in *Aequipecten irradians* (Sastry, 1965) and *Pecten maximus* (Comely, 1972); abnormal development associated with polyspermy or supernumerary sperms (Comely, 1972 and Gruffydd and Beaumont, 1972); and mechanical damage to extremely fragile eggs by contact with a nylon sieve (Comely, 1972). Fortunately, none of these problems occurred during the rearing of *P. magellanicus.*

Abnormal larvae did appear in the two minor spawnings whose volume of eggs was 1/10 or less than that of the major spawnings. Most of the larvae from these spawnings were conspicuously smaller than larvae from major spawnings (about 10 microns in length and height at the early straight-hinge stage). However, some deformities in shell formation were also observed. It seems likely these weak spawnings consisted of unripe or underdevelopd eggs.

The mass mortality suffered by larval populations at 19° C may indicate that this temperature is close to the upper limit of thermal tolerance for larvae. Dickie (1958) found that lethal temperatures for adult *P. magellanicus* ranged from 21° C to 23.5° C, depending on acclimation. The true cause of death of the half-grown larvae at 19° C is unknown. Loosanoff and Davis (1963) observed that bivalve larvae reared at relatively high temperatures were more susceptible to

mortality from disease. Gruffydd and Beaumont (1972) found that temperatures of 18° C and higher favored bacterial and ciliate growth that decimated their *Pecten maximus* larval cultures well before metamorphosis. The fungus observed attacking dead *P. magellanicus* larvae in my cultures at 19° C may have started growing in living larvae but this is uncertain.

The extremely fragile nature of larval shells of *Pecten maximus* reported by Comely (1972) was not apparent in *P. magellanicus*. Larvae were washed routinely in nylon sieves with no detectable damage to their shells from the earliest straight-hinge stage onward.

One problem, common to bivalve larvae, noted in *P. magellanicus*, was a tendency of late stage larvae to stick to each other and to debris in the cultures. This tendency appeared suddenly, at the time larvae first descended to swim in large concentrations near the bottom. The stickiness may be associated with the first attempts at byssus formation by the larvae. This interpretation is also suggested by Gruffydd and Beaumont (1972), who describe the same phenomenon in *Pecten maximus*. The problem can be controlled by drastically reducing the food allotment of the larvae when the eyespot is first detected, that is just before the appearance of bottom seeking behavior. The food-cell concentration should approximate 5×10^3 to 1×10^4 cells/cc/day or less, depending on larval population density. This eliminates much of the bottom debris caused by mass wastage of excess food. Bacterial and protozoan growth is minimized. Larvae still feed efficiently with the relatively large velum at this stage and remain largely free of detritus. Newly-settled spat which climb up off the bottom should be alloted more food than pediveligers, as the tiny gill at first appears to be an inefficient feeding mechanism.

The differences in size of the right and left valves of pediveligers may have taxonomic importance. This observation, especially with respect to depth, seems to show a predisposition in larvae to the adult condition where the right valve is more nearly flat.

The observations of behavior at different salinities show that larvae might survive considerable incursion into estuaries. Also, a general lowering of salinities in coastal waters following heavy rains would not seriously affect them. Because of their bottom-seeking behavior at salinities near 20‰ and lower, larvae entering stratified estuaries might be transported some distance inland. It is also possible this behavior might indirectly cause mortalities by subjecting larvae to benthic predation or to entrapment in bottom debris before they are ready to settle.

Pediveligers appeared capable of delaying metamorphosis for at least a month. In contrast to larvae of *Mytilus edulis*, studied by Bayne (1965) *Placopecten* pediveligers did not gradually lose the velum during the period of delay of metamorphosis. Unlike *M. edulis*, the scallop larvae retained their swimming ability.

The experiments on settling behavior suggest a generalized thigmotactic response in pediveligers. This differs from the major trend of results in experiments on larval settlement in which highly specific biochemical or biophysical stimuli have been observed (Scheltema, 1961; Crisp, 1965, 1967; Wilson, 1968). Because conditions in my experiments were not sterile, there remains a possibility that larvae responded to microbial films associated with the stimulus objects. However, such stimuli should also have been present in the sea water and on the

glass surfaces of finger bowls. The extremely high mortality associated with fragments of glass microscope slides may have been caused by some toxic coating on the slides, which were fresh from a new box. Attachment of spat on the undersides of the stimulus objects may be a behavioral adaptation to escape certain types of epibenthic predators, for example crabs, which are known to take a heavy toll of bivalve spat (P. Chanley, Shelter Island Oyster Co., personal communication).

A number of factors encountered in culturing larvae of *P. magellanicus* indicate that this would be a prime species for commercial mariculture. First the fact that the sexes are separate eliminates the problem of poor viability accompanying self-fertilization (Sastry, 1965; Comely, 1972). Larvae grew rapidly with little mortality at 15° C and thrived on a diet of the easily cultured *Isochrysis galbana*. Extreme precautions involving sterility of rearing equipment (Comely, 1972; Gruffydd and Beaumont, 1972) were not necessary with *P. magellanicus*, although an antibiotic such as Sulmet, used at 50 to 100 ppm would be recommended as larvae approach the pediveliger stage and aggregate near the bottom of the culture container. A reduction in food concentration would also be beneficial at this time. The natural tendency of pediveligers to settle beneath solid objects can be exploited. Spat are thus easily caught, manipulated, and transported on artificial substrates.

Presently, the most serious obstacle to hatchery production of *P. magellanicus* spat is that gametes cannot be obtained out of season. The potential for mariculture of these scallops is also a function of growth of juveniles and adults under artificial and captive conditions. New approaches and techniques will be needed. At the present time, juvenile scallops, derived from my larval populations, are growing rapidly in a flowing laboratory sea water system at Woods Hole.

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Summary

(1) Sexually mature *Placopecten magellanicus* from Isles of Shoals, New Hampshire, were observed to spawn in nature at 14°–16° C. In the laboratory, spawning occurred from 10°–15° C.

(2) Average sizes of developmental stages were: eggs, 64 microns diameter; swimming gastrula, 69 microns long by 63 microns diameter; earliest straight-hinge veliger, 105 × 82 microns, with a hinge line of 81 microns. The umbo stage began in larvae exceeding 175 × 155 microns. Pediveligers averaged 279 × 242 microns with a depth of 127 microns, and were inequivalved, the left valve being larger.

(3) Development from the zygote to the swimming gastrula took 30–40 hours at 12° C. The straight-hinge veliger stage was reached in four days at temperatures between 12° and 18° C.

(4) Veligers reared at 15° C reached the pediveliger stage in 28 days, and the first spat was observed on the 35th day. Veligers reared at 19° C suffered a mass mortality when approximately half grown.

(5) Larvae remained viable at salinities as low as 10.5‰, and exhibited normal swimming from 16.9‰ to 30.0‰ in a 42 hour test.

(6) Larvae showed a thigmotactic settling response to shell fragments, small pebbles, and glass fragments. Predominant settling was on the undersides of these objects. Pediveligers appeared to delay metamorphosis until suitable physical substrates for settlement were encountered.

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